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The Land Snail genus Afrodonta (Mollusca: Pulmonata: Endodontidae)

by

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SYNOPSIS

Study of 567 adult and juvenile specimens resulted in the recognition of two new taxa, *Afrodonta connollyi* new species and *Afrodonta bilamellaris londonensis* new subspecies. The hypothesis is presented that *Afrodonta* is a polyphyletic structural grade derived from several stocks of *Trachycystis*, *s. l.* rather than being a monophyletic assemblage. New diagnoses and discussions of variation are presented for all 14 specific level taxa.

INTRODUCTION

The present review of *Afrodonta* was initiated in order to assess the affinities of African 'toothed' endodontids with Pacific Island taxa; to study the patterns of apertural narrowing in the species; and to determine the amount of intraspecific variation. It is based primarily upon the collections in the Natal Museum, Pietermaritzburg (hereafter NM), supplemented by study of types in the British Museum (Natural History) (hereafter BMNH), plus a few sets in the Field Museum of Natural History, Chicago (hereafter FMNH), and the Auckland Institute and Museum (hereafter AIM). While two new taxa, *Afrodonta connollyi* and *Afrodonta bilamellaris londonensis*, are described and a few new locality records provided, primary emphasis is on analysis and interpretation of structure.

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GENERAL DISCUSSION

All previous workers on *Afrodonta* (Melvill & Ponsonby, 1908; Burnup, 1912; Connolly, 1912, 1925, 1933, 1939) have raised the question of possible relationships to Pacific

Island species. Prior to dissection and detailed study of the latter, no answers were possible. None of the Polynesian species had been dissected, descriptions and illustrations were far less detailed than those of African species, and comparative material had not been available to the earlier workers.

I have completed a detailed revision of the Pacific Island endodontid taxa that will be published elsewhere. On the basis of this work I have no hesitation in stating that similarities between the South African and Pacific Island species are parallelisms or convergent in nature. Several differences in both shell structure and anatomy are fundamental. The shells of *Afrodonta* have enlarged nuclear whorls with reduced or fine radial apical sculpture; both the Pacific Island subfamilies have no enlargement of the nuclear whorls and more complex apical sculpture. *Afrodonta* species have much finer and more crowded postnuclear sculpture than any Pacific Island species. Form, position, and structure of the apertural denticles are quite different in Pacific Island taxa and rather uniform; in *Afrodonta* it is highly variable (see p. 347). Fragmentary anatomical data on *Afrodonta* was presented by Godwin-Austen (1908) and Connolly (1925, 1939). Unfortunately, radular characters are of little use in classification, but the partial illustration of the pallial cavity in *Afrodonta novemlamellaris* given by Connolly (1925: 140, fig. 9, A) is sufficient to classify the genus. In possessing a complete and reflected ureter, *Afrodonta* (also *Trachycystis*, see Connolly, 1925: 146, 147, and Watson, 1934: pl. 20, fig. 11, pl. 21, fig. 39) is immediately recognizable as being phylogenetically distinct from the Pacific Island Endodontinae, which completely lack a secondary ureter and have a different heart and kidney configuration. Study of the genital system will be required before the exact affinities and subfamily position of *Afrodonta* can be determined, but it is not a member of the Endodontinae. Relationship with *Trachycystis* is discussed later.

Study of conchological variation in the Pacific Island species resulted in concluding that a syndrome of minor changes in shell growth pattern marks 'adulthood'; that measurements of adult shells showed a normal frequency distribution in regard to any character measured; and that size differences between populations within a species were very small. Despite having only fragmentary portions of original field collections available, measurements on adults of *Afrodonta* from different localities (Tables II and III) conform to this pattern. Only the populations of *A. novemlamellaris* and *A. bilamellaris* appear to show significant size and shape variation. *A. novemlamellaris* has less distinctly marked 'adult' characters, i.e. little body whorl descension, no change in ribbing, barely decoiling umbilicus, so that inclusion of subadults in the samples may account for the variation. *A. bilamellaris* may show extensive local differentiation. Other species appear quite uniform in size, shape, and apertural structure.

All measurements were made at 32× magnification with an ocular micrometer, using a Leitz stereoscopic dissecting microscope, and are accurate to 0·015 mm. In Tables II and III, data is recorded in millimeters as mean, standard error of the mean, and range of measurements, listed as 1·38 ± 0·028 (1·32–1·45). Ratios were calculated directly from the micrometer unit readings. Whorls were counted to the nearest eighth, with a '+' or a '−' indicating obvious departures from an exact figure. Table I summarizes the observed range of variation in all measured adult specimens. The column headed 'specimens examined' indicates the total number of adults and juveniles examined, not the number of adults

TABLE I

RANGE OF VARIATION IN AFRODONTA

	Number of specimens	Height	Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio	Pr	C	P
novemlamellaris	56	0.75(0.63-0.92)	1.27(1.10-1.45)	0.589(0.559-0.636)	4 1/4-(3 7/8-4 7/8)	0.26(0.21-0.41)	4.90(3.52-5.84)	2	1	4-5-7-2-3
farquhari	52	0.78(0.72-0.87)	1.38(1.30-1.46)	0.572(0.535-0.630)	4-(4-4 1/2)	0.26(0.23-0.31)	5.19(4.68-5.79)	2	1	3 4
burnupi	5	0.73(0.66-0.72)	1.40(1.37-1.45)	0.500(0.476-0.518)	4-(4-4 1/8)	0.46(0.44-0.48)	3.02(2.93-3.26)	2	1	0
connollyi	6	0.80(0.66-0.91)	1.52(1.32-1.64)	0.523(0.519-0.550)	4 1/4-(4-4 5/8)	0.38(0.33-0.43)	3.99(3.75-4.38)	2	0-1	0
acinaces	128	0.77(0.71-0.84)	1.47(1.35-1.60)	0.524(0.494-0.551)	4 1/2-(4 1/8-4 7/8)	0.57(0.49-0.64)	2.61(2.46-2.83)	1 two tubercles	1	2 bifurcated
rotula	23	0.83(0.76-0.94)	1.75(1.61-1.89)	0.471(0.438-0.523)	4 5/8-(4 1/4-5 1/8)	0.67(0.58-0.76)	2.62(2.50-2.80)	1	0	2
trilamellaris	21	0.73(0.66-0.79)	1.41(1.28-1.50)	0.515(0.488-0.529)	4(3 3/4-4 1/4)	0.52(0.43-0.56)	2.75(2.68-3.00)	1	1	1
bilamellaris bilamellaris	72	0.90(0.81-0.99)	1.59(1.50-1.71)	0.561(0.532-0.596)	4 1/2-(4 1/4-4 7/8)	0.44(0.38-0.51)	3.68(3.33-4.00)	1	0	1
bilamellaris londonensis	4	0.70(0.64-0.76)	1.34(1.30-1.37)	0.526(0.494-0.554)	4 1/8(4-4 1/4)	0.36(0.33-0.38)	3.71(3.52-4.15)	1	0	1
unilamellaris	34	0.70(0.66-0.76)	1.41(1.23-1.50)	0.500(0.471-0.533)	4 1/8-(3 7/8-4 1/4)	0.34(0.30-0.38)	4.14(3.72-4.50)	1	0	0
inhluzaniensis	85	0.84(0.76-1.00)	1.43(1.33-1.51)	0.584(0.523-0.663)	4-(3 3/4-4 3/8)	0.34(0.31-0.41)	4.21(3.60-4.60)	0	0	2
introtuberculata	78	0.78(0.76-0.81)	1.89(1.81-1.96)	0.424(0.403-0.495)	5 1/8-(5-5 3/8)	0.70(0.66-0.77)	2.70(2.49-2.80)	0	0	two tubercles
bimunita	1	1.17	1.97	0.600	5 1/4	0.61	3.24	0	0	two rows of tubercles
kempi	2	0.98(0.97-0.99)	1.67(1.60-1.74)	0.587(0.566-0.608)	4 1/2	0.44(0.39-0.48)	3.85(3.66-4.04)	0	0	two transverse calluses plus one tubercle

TABLE II

LOCAL VARIATION IN AFRODONTA

	Number of specimens	Height	Diameter	H/D Ratio	Whorls	Umbilicus	D/U Ratio
novemlamellaris Grahamstown	4	0.69±0.031 (0.63-0.77)	1.81±0.028 (1.10-1.23)	0.583±0.0147 (0.562-0.626)	4+ (3 7/8-4 1/4)	0.23±0.008 (0.21-0.25)	5.02±0.062 (4.80-5.15)
Kimberly	5	0.84±0.028 (0.77-0.92)	1.36±0.039 (1.25-1.45)	0.619±0.0044 (0.613-0.636)	4 1/2+ (4 1/4-4 7/8)	0.29±0.033 (0.21-0.41)	4.79±0.372 (3.52-5.84)
Mt. Vengo	8	0.73±0.009 (0.69-0.77)	1.28±0.012 (1.23-1.33)	0.571±0.0039 (0.559-0.586)	4 1/8- (4-4 1/4)	0.26±0.005 (0.23-0.28)	4.91±0.118 (4.59-5.64)
farquhari Grahamstown	4	0.80±0.016 (0.76-0.82)	1.38±0.028 (1.32-1.45)	0.580±0.0053 (0.568-0.590)	4 1/8+ (4-4 1/2)	0.26±0.013 (0.23-0.30)	5.27±0.170 (4.89-5.71)
Kowie	7	0.79±0.018 (0.72-0.87)	1.38±0.018 (1.30-1.45)	0.569±0.0110 (0.541-0.630)	4 1/8- (4-4 1/4)	0.27±0.010 (0.23-0.30)	5.06±0.133 (4.72-5.64)
Happy Valley, Port Elizabeth	8	0.78±0.012 (0.74-0.84)	1.36±0.017 (1.32-1.46)	0.571±0.0059 (0.535-0.602)	4- (4-4 1/8)	0.26±0.009 (0.25-0.31)	5.25±0.148 (4.68-5.79)
burnupi	5	0.73±0.012 (0.66-0.72)	1.40±0.014 (1.37-1.45)	0.500±0.0073 (0.476-0.518)	4+ (4-4 1/8)	0.46±0.006 (0.44-0.48)	3.02±0.060 (2.93-3.26)
connollyi Cathkin Peak	3	0.78±0.071 (0.66-0.91)	1.48±0.095 (1.32-1.64)	0.524±0.0143 (0.500-0.550)	4 1/4 (4-4 5/8)	0.37±0.029 (0.33-0.43)	3.98±0.070 (3.85-4.09)
Tugela Estates	3	0.81±0.022 (0.79-0.86)	1.55±0.050 (1.48-1.64)	0.521±0.0012 (0.519-0.523)	4 1/8- (4-4 3/8)	0.39±0.024 (0.35-0.43)	3.99±0.156 (3.75-4.38)
acinaces Van Reenen	11	0.77±0.014 (0.71-0.84)	1.47±0.026 (1.35-1.60)	0.524±0.0048 (0.494-0.551)	4 1/2+ (4 1/8-4 7/8)	0.57±0.016 (0.49-0.64)	2.61±0.030 (2.46-2.83)
rotula Fernkloof	4	0.81±0.030 (0.76-0.89)	1.78±0.036 (1.73-1.89)	0.453±0.0085 (0.438-0.469)	4 5/8- (4 1/2-4 7/8)	0.74±0.018 (0.67-0.76)	2.54±0.012 (2.50-2.56)

TABLE III

LOCAL VARIATION IN AFRODONTA

	Number of specimens	Height	Diameter	H/D Ratio	Whorls	Umbilicus	D/U Ratio
trilamellaris Dargle	10	0.73±0.013 (0.66-0.79)	1.41±0.022 (1.28-1.50)	0.515±0.0044 (0.488-0.529)	4 (3 3/4-4 1/4)	0.52±0.012 (0.43-0.56)	2.75±0.030 (2.68-3.00)
bilamellaris Edendale Falls	6	0.86±0.030 (0.81-0.97)	1.54±0.025 (1.50-1.63)	0.557±0.0107 (0.532-0.596)	4 1/2- (4 1/4-4 3/4)	0.41±0.009 (0.38-0.44)	3.81±0.057 (3.64-4.00)
Keurbooms	4	0.95±0.022 (0.89-0.99)	1.65±0.029 (1.60-1.71)	0.572±0.0081 (0.567-0.587)	4 1/2+ (4 1/2-4 3/4)	0.46±0.021 (0.43-0.51)	3.57±0.104 (3.36-3.77)
bilamellaris londonensis	4	0.70±0.024 (0.64-0.76)	1.34±0.014 (1.30-1.37)	0.526±0.0124 (0.494-0.554)	4 1/8 (4-4 1/4)	0.36±0.012 (0.33-0.38)	3.71±0.148 (3.52-4.15)
unilamellaris Mfongosi	7	0.70±0.013 (0.66-0.76)	1.41±0.035 (1.23-1.50)	0.500±0.0078 (0.471-0.533)	4 1/8- (3 7/8-4 1/4)	0.34±0.011 (0.30-0.38)	4.14±0.102 (3.72-4.50)
inhluzaniensis Cathedral Park	11	0.86±0.018 (0.77-1.00)	1.43±0.015 (1.33-1.51)	0.601±0.0071 (0.575-0.663)	4 1/8+ (4-4 3/8)	0.36±0.009 (0.31-0.41)	4.02±0.092 (3.60-4.60)
Inhluzani	3	0.83±0.015 (0.81-0.86)	1.43±0.020 (1.40-1.46)	0.585±0.0087 (0.570-0.600)	4+ (4-4 1/4)	0.32±0.005 (0.31-0.33)	4.41±0.083 (4.25-4.53)
Van Reenen	8	0.85±0.023 (0.82-0.89)	1.43±0.013 (1.37-1.48)	0.591±0.0064 (0.568-0.615)	4 1/8- (4-4 1/4)	0.34±0.007 (0.31-0.36)	4.28±0.061 (4.09-4.52)
Mkolombe	8	0.80±0.081 (0.76-0.82)	1.42±0.015 (1.37-1.48)	0.559±0.0055 (0.523-0.571)	3 7/8 (3 3/4-4 1/8)	0.33±0.005 (0.31-0.35)	4.34±0.053 (4.10-4.58)
introtuberculata Nottingham Road	9	0.78±0.006 (0.76-0.81)	1.89±0.018 (1.81-1.96)	0.424±0.0091 (0.403-0.495)	5 1/8+ (5-5 3/8)	0.70±0.012 (0.66-0.77)	2.70±0.033 (2.49-2.80)

measured. The summary of apertural dentition follows a tripartite apertural nomenclature, dividing the aperture into three zones: parietal wall or area appressed to the preceding whorl; columellar wall or area that forms the umbilical cavity sides; and palatal wall or area that forms the outer area of the last whorl. For each zone I have indicated the number of lamellae and/or tubercles. Where counts varied, an underlined figure, such as in '0–1', indicates that there is one lamella present in less than one-third of the specimens seen. A figure such as '4–5 + 2–3' indicates that there are usually four, occasionally five, lamellae and two or three accessory traces. Unusual alterations such as bifurcation or callus formation are specifically stated. This is the same system I used in summarizing data in the Pacific Island taxa reviews and will facilitate direct comparisons.

There are relatively clear-cut and sharp differences between the species in size, form, or apertural dentition. Identification of specimens is possible either by comparing measurements and lamellar counts against the summary in Table I or by using the artificial key (p. 349). Previous workers had provided excellent illustrations and descriptions that enabled species identification, but no data were available on size and shape variation. The availability of better microscopes and illumination allows description of sculptural characters more adequately, but the main purpose in providing new diagnoses of the species is to focus on the great variation in denticle structure shown by the different species. While the number of apertural denticles in the toothed endodontids is a highly variable character, the shape, relative length, growth pattern, width, and position of denticles are highly conservative characters. Description of these features is necessary in order to comment on the probable phylogeny of *Afrodonta* species.

While *Afrodonta* is a convenient unit of classification, I have no doubt that anatomical studies will demonstrate it is a polyphyletic assemblage representing a grade of structure rather than a monophyletic clade. Species now included in *Afrodonta* probably have been derived independently from several stocks of *Trachycystis*, *s. l.* While some species seem to be phyletically related to each other, *A. connollyi* to *A. burnupi*, *A. farquhari* to *A. novemlamellaris*, and possibly *A. bimunita* to *A. kempi*, there are few similarities between species pairs and numerous indications of separate derivations.

Part of the evidence is not direct, but is based upon trends of variations found in Pacific Island endodontids; part of the evidence is indirect, based upon non-concordance of structures; and part of the evidence comes from growth data deduced from observations made in the course of this study. No preserved specimens were available to me, yet anatomical data furnish the best possibility for verifying or disproving my hypothesis.

There is no experimental evidence concerning the functional significance of apertural protrusions in land snails, but probably they decrease predation by arthropods. Such denticles have developed many times in minute litter-dwelling endodontids. In the two Pacific Island subfamilies of endodontids, essentially all species of Endodontinae have apertural denticles, with the smaller species having the aperture narrowed more; in the Charopinae, apertural denticles have evolved several different times, usually in more specialized lineages. In the Endodontinae, loss or reduction of apertural denticles is secondary; in the Charopinae, development of such denticles is secondary. *Trachycystis*, *s. l.*, is a derivative from the 'Charopinae' lineage. While this has no necessary bearing on the

Afrodonta problem, it does indicate that possession of apertural denticles is not necessarily primitive.

In all Pacific Island taxa with denticles, these are present at hatching. There is continuous posterior resorption and anterior addition during shell growth. The denticles retain essentially the same position relative to the lip edge. An alternative method of growth is seen in other land snail families, such as the Corillidae, where denticles are formed in one area, shell growth proceeds for about one-quarter to one-third whorl, a new set of denticles is formed, and only then is the old set resorbed by the animal. With this pattern, there is a continually shifting relationship between the lip edge and denticle position. *Afrodonta introtuberculata* (see p. 361) clearly has the second type of denticle. There is some evidence that *A. kempi* and *A. bimunita* may share this. Other *Afrodonta* have denticle structure consistent with continuous deposition and resorption. The two types of formation are incompatible with monophyly. On this feature alone, *Afrodonta* contains at least two lineages.

While 'Cope's Law' concerning size increase during phyletic evolution generally holds, many examples of secondary decrease in size have been documented by Rensch and others. The swollen appearance of apical whorls in *Afrodonta*, which seems to be most pronounced in the smaller species, is consistent with selection for smaller adult size. Changes in embryonic whorl size lag behind selection for reduced postembryonic growth. Such differential changes usually are found in size reduction series. I do not know whether the minute *Trachycystis* show any indication of disproportionately large nuclear whorls, since these species could not be examined. I would suspect that the minute species of the *Trachycystis pura* complex will show a similar alteration.

Such changes are not limited to shell structure. In the Pacific Endodontidae there are distinctive changes in the pallial complex associated with either size reduction or great increase in whorl number. Both serve to reduce the relative cross-sectional volume of the body whorl near the aperture. One of the most characteristic changes is for the rectal kidney arm to overlap the hindgut or even extend on to the parietal wall, covering the underside of the hindgut. If viewed from outside the body with the shell removed, the effect of this is for the rectal kidney arm to appear much reduced in size, since the hindgut is on the surface and hides from view the kidney portion shifted under the hindgut and on to the parietal wall. Connolly (1925: 140, 146, 147) figured pallial regions, viewed from the outside, of *Afrodonta novemlamellaris*, *Trachycystis soror* and *T. pura*. Watson (1934: pl. 20, fig. 11 and pl. 21, fig. 39) presented the same views of *T. bisculpta* and *T. delicata*. I consider it highly suggestive of size reduction that the three microspecies figured by Connolly (loc. cit.) have distinct rectal kidney arms while the two large species merely have the posterior quarter of the kidney reaching the hindgut, but no appreciable development of a rectal kidney arm. Unfortunately Connolly did not figure or describe the inside appearance of the pallial complex. Determining the extent of rectal kidney arm development and hindgut overlap will be crucial in trying to determine the origin and affinities of *Afrodonta* species.

Apical sculpture varies from prominent to essentially absent, *A. trilamellaris*, *A. burnupi* and *A. acinaces* having prominent radial sculpture on the apex. *A. connollyi* probably is derived from *A. burnupi* and lacks prominent sculpture. Other species show little or no trace of any apical sculpture. Many *Trachycystis* show equivalent range of variability in apical sculpture.

Analysis of the apertural dentition strongly suggests separate derivations. Apertural narrowing usually is most pronounced in the lower half of the aperture, since the foot, digestive and reproductive organs must be withdrawn into the shell through the upper third to half of the aperture. Hence in such dentate forms as the typical Pacific Island Endodontinae, the supraperipheral palatal and parietal lamellae are usually smaller than the lower denticles. This is clearly demonstrated in *A. novemlamellaris* (see Burnup, 1912: pl. XXIV, fig. 11, and Connolly, 1933: pl. VII, fig. 1). Loss of some palatal lamellae in *A. farquhari* accentuates the pattern. The above two species have 'typical' endodontid lamellae. *A. connollyi* and *A. burnupi* have two very large parietals, weak columellar and no palatal dentition. The parietals alone effectively narrow the aperture. *A. acinaces* has two recessed parietals and two highly modified palatals (see Connolly, 1933: pl. VII, fig. 13); *A. trilamellaris* differs in having a very broad palatal situated opposite a modestly elevated parietal; *A. rotula* has a single deeply recessed parietal and two moderately recessed, long palatals that are located on the peripheral and basal margin, effectively a tripartite narrowing; while *A. bilamellaris* has a very large parietal that is frequently bifid (see figs. 2, *a–d*) plus one large palatal at the baso-columellar margin. *A. unilamellaris* has only one low parietal that is medially located. It shows the least apertural narrowing by lamella formation. Except for *A. unilamellaris*, the degree of apertural narrowing is essentially equivalent. The mechanics vary, but the result is the same.

The remaining species of *Afrodonta* have only palatal structures. *A. inhluzaniensis* has two variable lamellate tubercles on the lower palatal wall. Probably they have the typical growth pattern. *A. introtuberculata* has two small tubercles that are replaced at intervals; *A. bimunita* has two rows of palatal tubercles; and *A. kempi* has two transverse palatal calluses plus one tubercle. While they provide comparatively slight apertural narrowing, *A. bimunita* and *A. introtuberculata* are the largest known species of *Afrodonta*. Possibly they are approaching the upper size range for predation by the arthropods presumably excluded by the apertural narrowing in the other species. *A. kempi* is smaller than *A. rotula*, for example, but its range in Kenya is considerably north of other species and ecological conditions probably are not exactly comparable.

The above survey indicates that narrowing of the aperture has been achieved in a variety of ways. The palatal wall has tubercles that are replaced at intervals (*bimunita* and *introtuberculata*); transverse calluses (*kempi*); slender and crescentic lamellae (*novemlamellaris* and *farquhari*); a broad and crescentic peripheral lamella (*trilamellaris*); a high and broadly expanded, twisted lamella at the baso-columellar margin (*bilamellaris*); short and broad lamellate tubercles (*inhluzaniensis*); recessed, long, bifurcated lamellae on periphery and basal margin (*acinaces*); long and low ridgelike lamellae at periphery and on basal margin (*rotula*); and no palatals (*connollyi, burnupi, unilamellaris*). The parietal lamellae are less varied, with two large lamellae that are crescentic posteriorly (*connollyi, burnupi, novemlamellaris, farquhari*); medial elevated to bifurcated lamella (*bilamellaris*); low and medial lamella, rounded above (*trilamellaris, unilamellaris*); very broad and deeply recessed single lamella (*rotula*); and one subperipheral low lamella with two supraperipheral tubercles (*acinaces*).

Position, form, length, and character of these lamellae are neither uniform nor derivable from the condition seen in other species. Similarities in low ridge-like lamellae are meaningless, since this can be the beginning of a high lamella or the end of a size reduction process. In contrast to the Pacific Island taxa, where lineages show clear patterns of denticle change, the species of *Afrodonta* suggest a variety of experiments at developing an efficient method of apertural narrowing.

Afrodonta connollyi could be interpreted as either an enlarged derivative of *A. burnupi*, or the latter as a smaller descendant of the former. The reduced apical sculpture in *A. connollyi* suggests that the former alternative is more likely. *A. farquhari* may be a secondarily enlarged derivative from *A. novemlamellaris*. None of the other species shows sufficient similarities in apertural denticle placement and formation to be closely related, although *A. bimunita* and *A. introtuberculata* show some similarities in shape.

It is possible that seven or eight separate acquisitions of apertural denticles are involved. I consider that four or five separate derivations are probable. Unquestionably the difference between continuous tooth deposition and resorption in most species, and forming of successive barriers in some species, indicates an absolute minimum of two derivations. Watson (1934) demonstrated significant anatomical differences between species groups of *Trachycystis* and recognized ten subgenera. Dissection of the various minute species of *Trachycystis* and several *Afrodonta* will be required in order to substantiate or disprove the hypothesis of multiple derivations.

Until such studies are possible, retention of *Afrodonta* as a unit of classification is a practical procedure. Despite adopting this alternative, I consider that *Afrodonta* is a grade of structure and not a monophyletic assemblage. As such, I have given only a very short and generalized generic description that will serve to distinguish it from extralimital taxa.

Genus *Afrodonta* Melvill & Ponsonby

Afrodonta Melvill & Ponsonby, 1908. Ann. Mag. Nat. Hist. (8) **1**: 133–136.

Minute endodontoid species in which various tubercles, calluses, and lamellae serve to narrow the shell aperture. Body whorl generally laterally compressed, strongly rounded above. Umbilicus narrowly to broadly open. Apex slightly to moderately swollen, with or without radial sculpture. Postnuclear whorls with very fine radial ribs, often not significantly larger than microradial riblets, usually too fine and numerous for accurate counting. Anatomy unknown, except for radulae of a few species and kidney shape in one species.

Type species. Afrodonta bilamellaris Melvill & Ponsonby, 1908, by subsequent designation of Burnup (1912: 335).

Fourteen species and subspecies, including two described below, are included. All are minute, with a median mean diameter of less than 1·5 mm. The extremes of adult size in measured material are 1·10 mm and 1·97 mm. Of the slightly more than 100 described species of *Trachycystis*, 14 are between 2 and 3 mm in maximum diameter, while eight species—*T. rudicostata* Connolly, 1922; *T. soror* Connolly, 1922; *T. macdowelli* Connolly, 1922; *T. venatorum* Connolly, 1932; *T. ferarum* Connolly, 1932; *T. vengoensis* Connolly, 1922; *T. spissisculpta* Connolly, 1932; *T. pura* Connolly, 1922—fall within the size range of *Afrodonta*. Quite possibly some of these might have minute, deeply recessed denticles within the aperture, but examination of these species was outside the scope of this survey.

Most species have been found only within the Republic of South Africa, but *A. acinaces* and *A. novemlamellaris* have been reported from Mt. Panga (= Mt. Vengo), Moçambique and *A. kempi* is known only from localities in Kenya. More complete distributional records are given in Connolly (1939). I list only material actually examined during this study.

An artificial key to the species follows.

KEY TO THE GENUS *AFRODONTA*

1. Apex depressed beneath level of penultimate whorl .. 2
   Apex flat or elevated .. 3
2. Apex deeply sunken; H/D ratio about 0·590; two rows of five palatal tubercles .. **Afrodonta bimunita** Connolly, 1939
   Apex slightly depressed; H/D ratio about 0·410; palatal wall with two deeply recessed tubercles .. **Afrodonta introtuberculata** Connolly, 1933
3. Parietal wall with lamellae .. 5
   Parietal wall without lamellae .. 4
4. Palatal wall with two large lamellae near aperture; Natal .. **Afrodonta inhluzaniensis** (Burnup, 1912)
   Palatal wall with two transverse calluses, plus one tubercle recessed one quarter whorl; Kenya .. **Afrodonta kempi** (Connolly, 1925)
5. Parietal lamellae 2 .. 6
   Parietal lamellae 1 .. 9
6. No lamellae on outer palatal wall .. 7
   Several lamellae on outer palatal wall .. 8
7. Upper parietal distinctly smaller than lower; D/U ratio about 3·00 .. **Afrodonta burnupi** Connolly, 1933
   Upper parietal distinctly larger than lower; D/U ratio about 3·75–4·00 .. **Afrodonta connollyi,** new species
8. Palatal lamellae 3 with one accessory trace **Afrodonta farquhari** (Burnup, 1912)
   Palatal lamellae normally 5, with two accessory traces .. **Afrodonta novemlamellaris** (Burnup, 1912)
9. Palatal and/or columellar lamellae present .. 10
   No palatal or columellar lamellae present **Afrodonta unilamellaris** Connolly, 1933
10. Outer palatal wall without lamellae .. 11
    Outer palatal wall with one or more lamellae .. 12
11. Parietal lamella smaller, rarely bifid; basocolumellar margin with tubercle or short lamella (fig. 1, *a*) **Afrodonta bilamellaris bilamellaris** Melvill & Ponsonby, 1908
    Parietal lamella large, strongly bifid posteriorly; basocolumellar margin with broad, twisted lamella .. **Afrodonta bilamellaris londonensis,** new subspecies
12. Palatal lamellae 2 .. 13
    Only 1 palatal lamella .. **Afrodonta trilamellaris** Melvill & Ponsonby, 1908
13. Parietal wall with 2 tubercles above lamella; a broad columellar lamella; spire flat .. **Afrodonta acinaces** Connolly, 1933
    Parietal wall without accessory tubercles; no columellar lamella; spire slightly and evenly elevated .. **Afrodonta perfida** (Burnup, 1912)

Afrodonta novemlamellaris Burnup, 1912

Afrodonta novemlamellaris Burnup, 1912. Ann. Natal Mus., **2**: 341–342, pl. XXIV, figs. 11–13. Grahamstown, Kowie, King William's Town, Cape Province—Connolly, 1933, Ann. Natal Mus., **7**: 146, pl. VII, fig. 1. Ntimbakulu, Natal.—Connolly, 1939, Ann. S. Afr. Mus., **33**: 253–254, figs. 19 (4), 20. Kimberley, Cape Province.

Endodonta (*Afrodonta*) *novemlamellaris* (Burnup), Connolly, 1912. Ann. S. Afr. Mus., **11** (3): 128. Connolly, 1925. Trans. Roy. Soc. S. Afr., **12**: 139–140, figs. 9A, B. Mt. Vengo (=Mt. Panga), Moçambique.

Diagnosis. Shell minute, diameter 1·10–1·45 mm (mean 1·27 mm), with $3\frac{7}{8}$ to $4\frac{7}{8}$ tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl not descending more rapidly, spire protrusion about one-third body whorl width, H/D ratio 0·559–0·636 (mean 0·589). Apical whorls slightly swollen, strongly granulose, without definite microreticulation. Postnuclear whorls with very fine, crowded, radial riblets, crossed by much finer and more crowded spiral riblets. Umbilicus very narrow, 'U'-shaped, barely decoiling, contained 3·52–5·84 times (mean 4·90) in the diameter. Sutures deep, whorls strongly rounded above, evenly rounded on outer and basal margin with very slight lateral flattening. Parietal lamellae 2, extending slightly more than one-quarter whorl: upper parietal a narrow, bladelike lamella, expanded above on elevated posterior half, descending sharply to anterior third which is a low ridge, reaching lip margin; 2nd parietal slightly broader and a little higher, with gradual anterior descension, extending slightly further than apertural edge. Columellar wall with a single, high, crescentic lamella, extending one-eighth whorl, with sharp anterior descension, slanting at a 50° angle from the plane of coiling toward baso-columellar margin. Palatal lamellae 4 to 7, usually (67%) 5, with two, rarely (4%) three, superior traces: palatals low, short, bladelike lamellae with gradual anterior descension, recessed within aperture, narrow; lower 3 crescentic, upper pair flatter on top. Palatal traces short, inconspicuous, threadlike ridges located between upper palatal and palatal-parietal margin.

Afrodonta novemlamellaris is immediately recognizable by its protruding spire and many palatal lamellae. *A. farquhari* has only three (rarely four) palatals and is a trifle larger with the apertural denticles reduced in size. No other species have more than two palatals.

Holotype. Grahamstown, Cape Province. Collected by J. Farquhar. British Museum (Natural History) number 1912.3.25.4.

Material. Cape Province: Mountain Drive, Grahamstown (10 specimens, NM, FMNH 159051); Grahamstown (6 specimens, BMNH 1912.3.25.4, BMNH 1937.12.30.2703, BMNH 1937.12.30.2786–9); Trappes Valley, Bathurst (2 specimens, NM); Kimberley (5 specimens, NM, BMNH 1937.12.30.2784–5). Natal: Ntimbankulu (11 specimens, NM, BMNH 1937.12.30.2704). Moçambique: Mt. Vengo (= Mt. Panga) (22 specimens, AIM, BMNH 1937.12.30.2705–23).

Remarks. Afrodonta novemlamellaris shows moderate variation in apertural dentition. Of 27 adult specimens with cleared apertures, 20 had 5 major palatals and two traces; 2 had 6 majors; 2 had 7 majors, 1 had only 4 majors, and 2 had 5 majors with three traces. The accessory trace was located between the 4th and 5th palatals.

A. farquhari could be derived from *A. novemlamellaris* through size reduction of the parietals and columellar, plus loss of some palatals. It is barely possible that they are not distinct, but that *A. farquhari* is a gerontic growth stage or mutation of *A. novemlamellaris.*

Reduction and loss of apertural denticles have been observed in several Pacific Island endodontids (unpublished data). The two *Afrodonta* differ only in tooth size and number with a slight average size increment for *A. farquhari*. Both species have been collected at Kowie, Grahamstown, and Bathurst. In each case, all adult *A. farquhari* are larger than the *A. novemlamellaris* from the same locality. Juveniles with typical *A. farquhari* dentition were found at Kowie so that the probability of gerontic reduction is very small. The possibility of mutational difference is larger.

Data in Table I concerning the size differences between the two species is somewhat misleading. The overlap in height and diameter is caused by a single sample of very large *A. novemlamellaris* from Kimberley. These shells (see Table II) have the size of *A. farquhari*, but the dentition of *A. novemlamellaris*. Remaining samples of the latter contain specimens with a maximum height of 0·77 mm, and a maximum diameter of 1·33 mm. This greatly reduces the extent of overlap between the two taxa.

Of all *Afrodonta*, this species must closely approximates the apertural dentition found in Pacific Island taxa, but the exact formation of the denticles differs. Since the most similar species are still undescribed, detailed comparisons must be deferred.

Afrodonta farquhari (Burnup, 1912)

Endodonta (*Afrodonta*) *farquhari* Burnup 1912. Ann. Natal Mus., **2**: 339–340, pl. XXIV, figs. 7–10. Grahamstown, Port Elizabeth, Kowie, Bathurst, Cape Province.—Connolly, 1912. Ann. S. Afr. Mus., **11** (3): 128.
Afrodonta farquhari (Burnup), Connolly, 1938. Ann. S. Afr. Mus., **33**: 253.

Diagnosis. Shell very small, diameter 1·20–1·46 mm (mean 1·36 mm), with $3\frac{5}{8}$ to $4\frac{1}{2}$ tightly coiled whorls. Apex and spire strongly and evenly elevated, body whorl descending slightly more rapidly, spire protrusion more than one third body whorl width, H/D ratio 0·535–0·630 (mean 0·570). Apical whorls minutely granulose, slightly swollen. Postnuclear whorls with very fine and crowded radial riblets with barely visible secondary spiral riblets. Umbilicus very narrow, 'U'-shaped, barely decoiling, contained 4·68–5·71 times (mean 5·16) in the diameter. Sutures shallow, whorls evenly rounded on outer and basal margin. Parietal lamellae 2, high, crescentic, upper parietal relatively short, extending three-sixteenths of a whorl, with gradual descension to anterior threadlike third, posterior third high, lamellate, slightly expanded above; lower parietal much higher, extending over one-quarter whorl, laterally sinuately twisted posteriorly with very gradual descension until anterior eighth, reaching past lip margin. Columellar wall with single, high, threadlike ridge, moderately recessed within aperture, situated near columellar-basal margin and slanting about 45° downward from plane of coiling. Palatal lamellae 3, short, low lamellae, with one superior trace. Lower palatal at baso-columellar margin, extending less than one-eighth whorl, moderately recessed within aperture; 2nd palatal slightly below periphery, shorter, equally recessed; upper palatal slightly supraperipheral in position, lying opposite upper parietal tooth, more deeply recessed. Palatal trace an inconspicuous, threadlike ridge situated just below palatal-parietal margin, deeply recessed within aperture.

Afrodonta farquhari is slightly larger, has fewer palatal lamellae and smaller parietals than in *A. novemlamellaris*. Otherwise the two species show no significant differences. Other species with two parietals either completely lack palatal dentition or have only a single palatal.

Holotype. Grahamstown, Cape Province. Collected by J. Farquhar. British Museum (Natural History) number 1912.3.25.3.

Material. Cape Province: Belmont, Grahamstown (5 specimens, AIM, FMNH 159055); Grahamstown (4 specimens, BMNH 1912.3.25.3, BMNH 1913.7.31.299–301); Signal Hill, East London (3 specimens, NM); Kowie (23 specimens, BMNH 1937.12.30. 2734–49, NM); Happy Valley, Port Elizabeth (6 specimens, BMNH 1937.12.30.2750–4); Port Elizabeth (6 specimens, NM); Trappes Valley, about 6 miles from Bathurst (5 specimens, NM).

Remarks. Data concerning the possibility of *A. farquhari* being a gerontic stage of *A. novemlamellaris* is presented under the discussion of that species. Without additional field collections, dissections, and raising specimens of *A. novemlamellaris* until death from old age it will not be possible to determine their relationships.

Variation between sets of *A. farquhari* from different localities was essentially nonexistent (Table II). Of 18 adults with cleared apertures, 2 had 4 palatals and 16 had 3 palatals. No analysis of dentition in juveniles was undertaken.

Afrodonta burnupi Connolly, 1933 (fig. 1, *e*)

Afrodonta burnupi Connolly, 1933. Ann. Natal Mus., 7: 148, pl. VII, figs. 9–11. Mkolombe Mts., Natal.—Connolly, 1939. Ann. S. Afr. Mus., 33: 252, fig. 19 (7) Partly.

Diagnosis. Shell smaller than average, diameter 1·37–1·45 mm (mean 1·40 mm), with 4 to 4⅛ tightly coiled whorls. Apex slightly protruding, spire barely elevated, protrusion about one-ninth body whorl width, last whorl descending slightly, H/D ratio 0·476–0·518 (mean 0·500). Apical whorls slightly swollen, sculpture of fine radial ribs and barely visible spiral riblets. Postnuclear whorls with very fine and crowded radial riblets whose interstices are one to two times their width. Microsculpture of one to two microradials between each pair of major ribs and slightly finer microspirals. Umbilicus broadly 'U'-shaped, regularly decoiling, contained 2.93–3·26 times (mean 3·02) in the diameter, margins weakly shouldered. Parietal lamellae 2, unequal in length, largest extending almost one-quarter whorl: upper high posteriorly, expanded, with gradual descension over anterior half to end recessed about one-sixteenth whorl from anterior end of lower parietal; 2nd gradually descending over anterior half to lip edge, posteriorly greatly elevated, more expanded and slightly higher than 1st. Columellar wall with single broadly rounded, cord-like ridge just above basal margin, rather deeply recessed and relatively short.

Afrodonta connollyi is most closely related, but differs in its much narrower umbilicus, in having the 1st parietal larger than the 2nd and extending much further anteriorly, plus the apical sculpture is noticeably reduced. In *A. burnupi* the upper parietal is never visible even in a tilted umbilicus view (fig. 1, *e*), while in *A. connollyi* it is visible even in normal position (fig. 1, *d*).

Description. Shell rather small, with slightly more than 4 tightly coiled whorls. Apex and early spire flat, lower spire and body whorl descending slightly, H/D ratio 0·476. Apical whorls 1½, first 1¼ whorls moderately swollen, last narrowing slightly. Apical sculpture of fine, relatively crowded radial riblets with very faint microspiral riblets. Postnuclear whorls with narrow, low, very crowded radial riblets, about 202 on the body whorl, whose

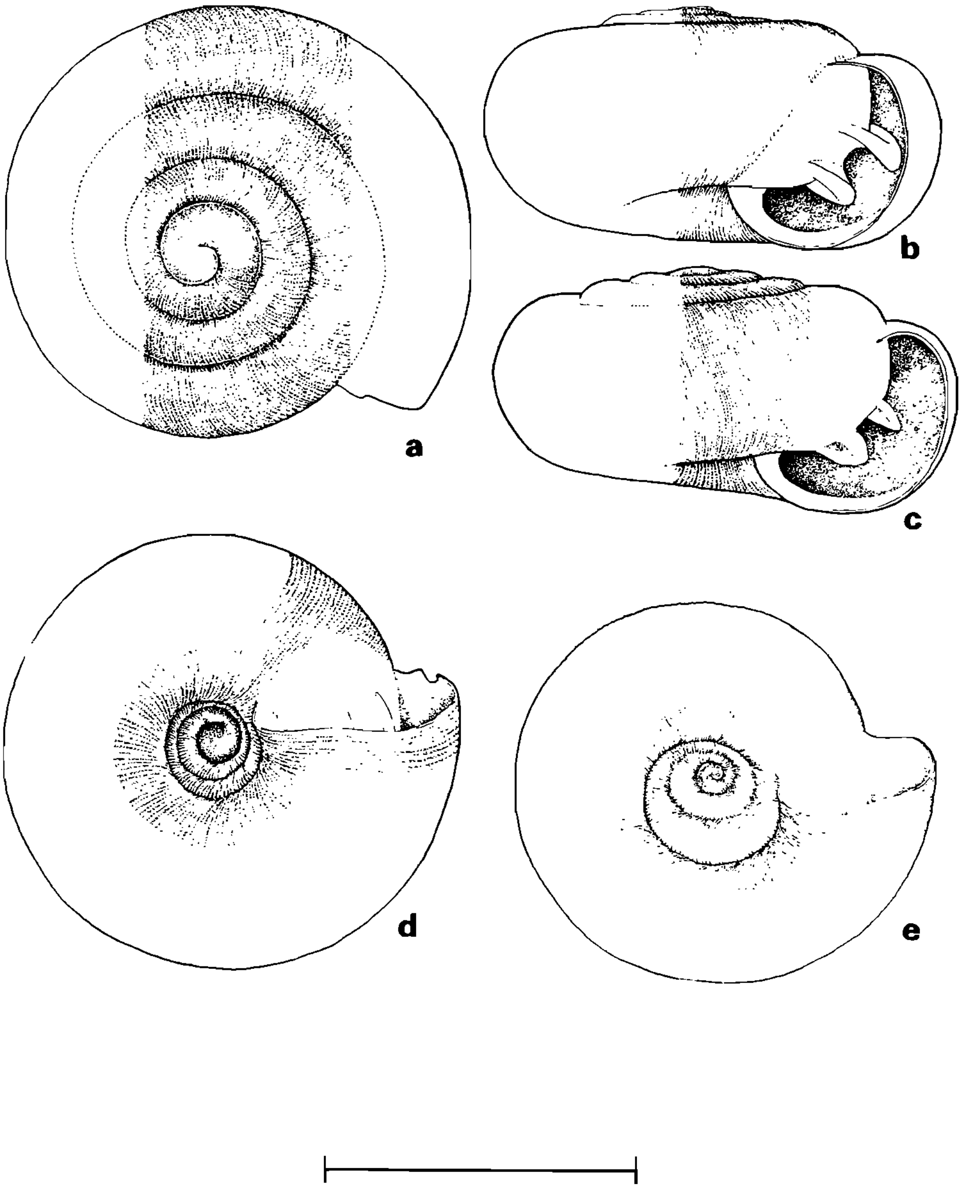

Fig. 1. *Afrodonta connollyi*, new species, holotype from Tugela Estates, Weenen, Natal: *a*, top view; *b–c*, side views showing tooth structure; *d*, bottom view. *Afrodonta burnupi* Connolly, paratype from Mkolombe Mt., Natal: *e*, bottom view tilted to show parietal lamella. Scale line equals 1 mm.

interstices are one to two times their width. Occasionally microspiral ribbing is visible, much more so in umbilicus, and there are one or two microradials between each pair of major ribs. Sutures deep, whorls strongly rounded above, somewhat compressed laterally with evenly rounded lower palatal and basal margin. Umbilicus cup-shaped, regularly decoiling, contained 3·00 times in the diameter, with slightly shouldered margins. Parietal wall with 2 high, crescentic lamellae, extending nearly one-quarter whorl: upper parietal with anterior half a low, narrow, gradually descending ridge, moderately recessed, becoming greatly elevated and broadly rounded posteriorly; lower parietal reaching to lip edge with anterior half gradually descending, becoming broadly expanded and higher posteriorly than 1st. Columellar wall with a low, broadly rounded cordlike ridge recessed one-sixteenth whorl within aperture, extending posteriorly less than one-sixteenth of a whorl. Palatal wall without dentition. Height of holotype 0·66 mm, diameter 1·38 mm.

Holotype. Mkolombe Mountains, Natal. Collected by H. P. Thomasset. British Museum (Natural History) number 1931.6.4.4.

Material. Mkolombe Mts., Natal (5 specimens, BMNH 1931.6.4.4, NM).

Remarks. All known material was collected in March 1926 by H. P. Thomasset. Specimens from Tugela River, Weenen, referred to this by Connolly (1933: 148) are described below as *Afrodonta connollyi*. Differences between the two are given in the diagnosis above.

The relatively prominent apical sculpture of *Afrodonta burnupi* and absence of palatal dentition effectively separate it from other species. *A. unilamellaris* is the only other species lacking palatal dentition. It differs in having only a single parietal lamella that is low and cord-like, a much narrower umbilicus, and smooth apical whorls. Conceivably it could be derived from the *burnupi-connollyi* by tooth reduction and loss of the apical sculpture.

Afrodonta connollyi, new species (fig. 1, *a–d*)

Afrodonta burnupi Connolly, 1933, Ann. Natal Mus., 7: 148—Tugela Estate, Weenen, Natal. Partly.—Connolly, 1939. Ann. S. Afr. Mus., **33**: 252.

Diagnosis. Shell average in size, diameter 1·32–1·64 mm (mean 1·52 mm), with 4 to 4⅝ tightly coiled whorls. Apex and spire slightly and evenly elevated, spire protrusion about one-eighth body whorl width, last whorl descending more rapidly, H/D ratio 0·519–0·550 (mean 0·523). Apical whorls 1⅜, very faint traces of radial sculpture visible except where worn. Postnuclear whorls with extremely fine and crowded radial sculpture, sometimes separable into microriblets and moderately larger major ribs, usually of equal fineness at 96× magnification. Umbilicus relatively narrow, 'U'-shaped, regularly decoiling, contained 3·75–4·38 times (mean 3·99) in the diameter, margins weakly shouldered. Parietal lamellae 2, extending posteriorly about three-sixteenths of a whorl: upper very high and thin posteriorly with gradual descension over anterior three-quarters to point just behind anterior end of lower; 2nd not as high posteriorly, elevated portion extending further anteriorly with sharper descension to point beyond lip edge. Columellar wall with (33%) or without (67%) a recessed, cord-like ridge just above baso-columellar margin. Palatal wall without traces of dentition.

Afrodonta burnupi differs in having a much wider umbilicus, the upper parietal shorter and much lower than the 2nd, and in having more prominent apical sculpture. *A. uni-*

lamellaris has a more protruded spire, only a single parietal lamella, and is slightly smaller in size.

Description. Shell of average size, with slightly more than 4⅛ tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0·522. Apical whorls slightly more than 1¼, a little swollen, very fine microreticulation visible under 96× magnification. Postnuclear whorls with very fine microriblets and only slightly larger radial ribs, not clearly enough differentiated for counting. Sutures deep, whorls strongly rounded above, compressed laterally with evenly rounded outer margin, umbilical margin weakly shouldered. Umbilicus relatively narrow, 'U'-shaped, regularly and slightly decoiling, contained 4·38 times in the diameter, margins shouldered. Parietal lamellae 2, extending posteriorly three-sixteenths of a whorl: upper very high, sinuately twisted posteriorly, with gradual anterior descension over anterior five-eighths until just before end when the descension accelerates; 2nd slightly lower and shorter posteriorly, more expanded above, with sharper anterior descension to point slightly beyond end of upper parietal. Columellar and palatal walls without dentition. Height of holotype 0·79 mm, diameter 1·51 mm.

Holotype. Hlonyana Bank, tributary of Tugela River, Tugela Estates, Weenen, Natal. Collected by H. P. Thomasset on 11 March 1928. Natal Museum.

Material. Tugela Estates, Weenen (3 specimens, NM, BMNH 1937.12.30.2728–9); Cathkin Peak, Drakensberg Mts. (3 specimens, NM, FMNH 159048).

Remarks. Four of the six specimens lacked any trace of a columellar ridge; one had a cord only slightly smaller than that found in *A. burnupi*; and one had a very small, deeply recessed trace. There was no noticeable variation in the parietal dentition.

While the type is unusual in having the narrowest umbilicus observed, in other respects it is quite typical and shows the best sculptural preservation.

Afrodonta acinaces Connolly, 1933

Afrodonta acinaces Connolly, 1933. Ann. Natal Mus., 7: 149, pl. VII, figs. 12–15. Van Reenen, Natal.—Connolly, 1939, Ann. S. Afr. Mus., 33: 253, fig. 19 (8).

Diagnosis. Shell of average size, diameter 1·35–1·60 mm (mean 1·47 mm), with 4⅛ to 4⅞ tightly coiled whorls. Apex and early spire flat, last whorl barely descending, spire protrusion about one-eighth body whorl width, H/D ratio 0·494–0·541 (mean 0·524). Apical sculpture of prominent, closely spaced (interstices twice their width) radial ribs, slightly less crowded at first, with very fine, barely visible, spiral microsculpture. Postnuclear whorls with low, rounded, vertically sinuated radial ribs, about 200 on the body whorl, whose interstices are less than 1½ times their width. Occasionally an extremely fine microreticulated sculpture of two to four microradials between each pair of majors can be seen. Umbilicus broadly 'U'-shaped, very widely open, regularly and rapidly decoiling, contained 2·46–2·83 times (mean 2·61) in the diameter. Sutures deep, whorls strongly rounded above and on umbilical margin with evenly rounded, compressed outer margin. Parietal wall with one short lamella and two isolated bumps, occasionally joined to form a second lamella: parietal lamella sub-peripheral, elevated, a broadly expanded and rounded ridge; slightly above periphery are two small knobs, anterior slightly recessed within aperture, round, very small, posterior recessed one-eighth whorl, three or four times the size of the front, irregular in shape. Columellar wall with single, broadly rounded, wide short lamella, recessed one-eighth whorl from aperture, extending less than one-eighth of a whorl inward. Palatal wall with 2 broad, threadlike lamellae, each with a medial depression dividing it into two ridges after anterior quarter, extending three-sixteenths of a whorl, plus a small, short (one-sixteenth of a whorl) ridgelike trace recessed over one-eighth whorl within aperture and extending posteriorly less than one-sixteenth of a whorl, located just below upper palatal margin.

Afrodonta acinaces is immediately recognizable by its bifurcated palatals, presence of 2 superior parietal bumps and strong apical sculpture. Other species with strongly sculptured apical whorls, *A. trilamellaris* and *A. burnupi*, immediately are separable by the broad columellar lamella of the former and 2 very high parietals in the latter.

Holotype. Van Reenen, Natal. Collected by H. C. Burnup. British Museum (Natural History) number 1931.6.4.2.

Material. Van Reenen (128 specimens, NM, BMNH 1931.6.4.2, FMNH 159052).

Remarks. Only the single collection by Burnup is known. Unfortunately most specimens seen were juvenile, and only the one set was measured. The slightly elevated and broadly expanded parietal is unique among described *Afrodonta* as are the bifurcated palatals. No Pacific Island taxa have palatals matching the structure of those in *Afrodonta acinaces*. Despite their relatively low profile, when combined with the high parietal they do an excellent job in narrowing the aperture.

Afrodonta rotula (Melvill & Ponsonby, 1907)

Trachycystis rotula Melvill & Ponsonby, 1907. Ann. Mag. Nat. Hist. (7), **19**: 99–100, pl. VI, figs. 12, *a*. Fern Kloof, Grahamstown, Natal.—Melvill & Ponsonby, 1908. Ann. Mag. Nat. Hist. (8), **1**: 135.
Endodonta (*Afrodonta*) *perfida* Burnup, 1912. Ann. Natal Mus., **2**: 337–339, pl. XXIV, figs. 1–6. New name for *Trachycystis rotula* Melvill & Ponsonby, 1907.—Connolly, 1912. Ann. S. Afr. Mus., **11** (3): 128.
Afrodonta perfida (Burnup). Connolly, 1939. Ann. S. Afr. Mus., **33**: 255.

Diagnosis. Shell quite large, diameter 1·61–1·89 mm (mean 1·76 mm), with 4¼ to 5⅛ tightly coiled whorls. Apex and spire strongly and evenly elevated, body whorl descending a little more rapidly, spire protrusion about one-third body whorl width, H/D ratio 0·438–0·523 (mean 0·471). Apical whorls smooth, with very faint traces of microreticulation, usually appearing as granulosities. Postnuclear whorls with narrow, lamellar, slightly protractively sinuated radial ribs, 159–208 (mean 182) on the body whorl, whose interstices are less than twice their width. Microsculpture of nearly co-equal radial and spiral riblets. Umbilicus broadly 'V'-shaped, widely open, regularly decoiling, contained 2·50–2·80 times (mean 2·62) in the diameter. Sutures deep, whorls strongly rounded above, slightly compressed laterally and on basal margin. Parietal wall with a single, broad, low, very deeply recessed lamella, anterior edge about one-eighth whorl from aperture, bluntly 'V'-shaped extending posteriorly for over three-sixteenths of a whorl, becoming moderately elevated posteriorly. Columellar wall without dentition. Palatal lamellae 2, extending three-sixteenths to one-quarter whorl, large, threadlike ridges, deeply recessed within aperture: lower palatal basal in position, slightly more prominent than the upper; upper palatal peripheral, lower and more broadly rounded.

Afrodonta trilamellaris has a very broad columellar and one broad, short palatal situated near aperture, while *A. perfida* lacks a columellar lamella, has two very long palatals and a deeply recessed parietal, is much larger in size and has a more elevated spire. *A. acinaces* is smaller, has the palatals divided medially, a prominent columellar and the parietal located near the lip edge.

Holotype. Fern Kloof, Grahamstown, Natal. Collected by J. Farquhar. British Museum (Natural History) number 1912.3.25.1.

Material. Fern Kloof, Grahamstown (23 specimens, NM, BMNH 1912.3.25.1, BMNH 1937.12.30.2790–2, AIM, FMNH 86263, FMNH 155939).

Remarks. In having a deeply recessed parietal, which can easily be overlooked by casual inspection, and two very long palatals, *Afrodonta rotula* is separated from other species. The smooth spire and widely open umbilicus mean that, in general appearance, only *A. acinaces*, *A. introtuberculata* and *A. trilamellaris* can be confused. *A. introtuberculata* has only two palatal tubercles, while differences from the others are covered in the diagnosis above.

Burnup (loc. cit.) proposed a substitute name for *A. rotula* under the impression that *Helix rotula* Hombron & Jacquinot, 1852, might be congeneric. The latter is an unidentifiable endodontid, supposedly from Mangareva, Gambier Islands. All Gambier Island endodontids belong to the Endodontinae so that even if identified, this species would be placed in a different genus.

Afrodonta trilamellaris Melvill & Ponsonby, 1908

Afrodonta trilamellaris Melvill & Ponsonby, 1908. Ann. Mag. Nat. Hist. (8), **1**: 134–135, pl. VII, figs. 7, *a*, *b*. Dargle, Natal.—Connolly, 1912. Ann. S. Afr. Mus., **11** (3): 128–129.—Connolly, 1939. Ann. S. Afr. Mus., **33**: 252, fig. 19(2).

Diagnosis. Shell smaller than average, diameter 1·28–1·50 mm (mean 1·41 mm), with 3¾ to 4¼ tightly coiled whorls. Apex barely emergent, early spire flat, last whorl descending slightly, spire protrusion about one-ninth body whorl width, H/D ratio 0·488–0·529 (mean 0·515). Apical sculpture of fine, crowded, radial riblets, whose interstices are 1 to 1½ times their width with barely visible microspiral riblets. Postnuclear whorls with narrow, rounded, low, vertically sinuated radial ribs, 157–203 (mean 173·7) on the body whorl, whose interstices are equal to their width. Very faint traces of microreticulation visible. Umbilicus widely open, cup-shaped, regularly decoiling, contained 2·68–3·00 times (mean 2·75) in the diameter. Margins slightly shouldered. Sutures deep, whorls strongly rounded above and on basal margin, evenly rounded on somewhat compressed lateral margin. Parietal lamella medial in position, a moderately elevated, broadly rounded ridge, extending posteriorly three-sixteenths of a whorl. Columellar wall with a very broad, flat ridge reaching on to basal lip, slightly recessed from aperture and extending posteriorly a little more than one-eighth whorl. Palatal wall with sub-medial, crescentic, very broad (0·15 mm) short ridge, extending one-eighth of a whorl, moderately recessed within aperture.

Afrodonta trilamellaris is distinguished primarily by its short and broad palatal lamella and very broad columellar lamella. *A. bilamellaris* has no columellar, a lamellate palatal located at the baso-columellar margin, and a much narrower umbilicus. *A. unilamellaris* has only a single low parietal.

Holotype. Dargle, Natal, South Africa. Collected by H. C. Burnup. British Museum (Natural History) number 1908.12.13.42.

Material. Natal: Dargle (21 specimens, NM, BMNH 1908.12.14.42, BMNH 1937.12.30.2793–4, FMNH 46437).

Remarks. Location of the very broad palatal opposite the reduced parietal effectively narrows the shell aperture. The other species with only a single palatal, *A. bilamellaris*, has it located at the baso-columellar margin. The broadly rounded palatal of *A. trilamellaris* is not matched by any other species and the transformation of the columellar into a broad callus is equally distinctive.

Only one collection of this species has been made.

Afrodonta bilamellaris bilamellaris Melvill & Ponsonby, 1908 (figs. 2, *a–b*)

Afrodonta bilamellaris Melvill & Ponsonby, 1908, Ann. Mag. Nat. Hist. (8), **1**: 134, pl. VII, fig. 6. Dargle, Edendale Falls, Natal.—Godwin-Austen, 1908. Ibid., p. 135, pl. VIII, fig. 2. Radula.—Connolly, 1912. Ann. S. Afr. Mus., **11** (3): 127–128. Tongaat, Enon Bush, Richmond, Hilton Road, Ntimbankulu, Natal.—Connolly, 1939. Ann. S. Afr. Mus., **33**: 251, fig. 19 (1). Sinkwazi and Winkle Spruit, Natal. Keurbooms River bush and Plettenberg Bay, Cape Province.

Diagnosis. Shell large, diameter 1·50–1·71 mm (mean 1·59 mm), with 4¼ to 4⅞ tightly coiled whorls. Apex and spire moderately and evenly elevated, spire protrusion about one-sixth body whorl width, body whorl descending more rapidly, H/D ratio 0·532–0·596 (mean 0·561). Apical whorls 1¼ to 1⅜, unworn examples with fine microreticulation, radials slightly more prominent than spirals at 96× magnification. Postnuclear whorls with very fine and crowded major radials and microradials, crossed by distinctly more crowded spirals. Umbilicus 'U'-shaped, slightly decoiling at first, last whorl more rapidly, contained 3·33–4·00 times (mean 3·68) in the diameter, margins strongly rounded. Sutures impressed, whorls strongly rounded above, compressed and evenly rounded laterally, with strongly rounded basal margin. Parietal wall with variable median lamella, extending posteriorly one-eighth to one-quarter whorl, posterior third to quarter high and crescentic, weakly expanded (fig. 2, *b*) to markedly bifid (fig. 2, *a*), with sharp to gradual descension over anterior two-thirds to three-quarters, termination varying from near lip edge to moderately recessed. Columellar wall without dentition. Palatal wall with single, moderately recessed, crescentic, narrow to broadly expanded tubercle situated just below baso-columellar margin and extending posteriorly less than one-eighth whorl.

The slightly smaller *Afrodonta bilamellaris londonensis* has both the parietal and palatal lamellae much larger and longer. *A. perfida* and *A. trilamellaris* have two denticles on the columellar and palatal wall and much wider umbilici; other *Afrodonta* have either two or no parietals.

Holotype. Dargle, Natal. Collected by H. C. Burnup. British Museum (Natural History) number 1908.12.14.54.

Material. Cape Province: Keurbooms River bush (4 specimens, BMNH 1937.12.30.2730–3). Natal: Ntimbankulu Hill (13 specimens, NM, FMNH 86262); Edendale Falls (8 specimens, BMNH 1908.12.14.54–5, Natal); Hilton Road (2 specimens, NM); Dargle (6 specimens, NM); Botanical Gardens, Pietermaritzburg (5 specimens, NM); Tongaat (8 specimens, NM); Enon Bush, Richmond (1 specimen, NM); Sinkwazi (5 specimens, NM); Nottingham Road (11 specimens, NM); Howick (9 specimens, NM).

Remarks. Considerable variation was seen in the length and posterior development of the parietal lamella. In 4 (9·1%) of 44 adults, it was distinctly bifid posteriorly (fig. 2, *a*), while in the remaining 40 it was only weakly to moderately expanded above (fig. 2, *b*). The bifid parietals were found in sets from Dargle (two specimens) and single specimens in larger sets of the normal form from Edendale Falls and Keurboom River bush.

Size differences between local populations (Table II) need to be investigated for significance. Larger field collections are required for this purpose, since most available sets contained one or two adults.

Afrodonta bilamellaris londonensis, new subspecies (figs. 2, *c–d*)

Diagnosis. Shell small, diameter 1·30–1·37 mm (mean 1·34 mm), with 4 to 4¼ tightly coiled whorls. Apex and spire moderately and evenly elevated, spire protrusion almost one-fifth body whorl width, last whorl descending more rapidly, H/D ratio 0·494–0·554 (mean 0·526). Apical whorls about 1⅜, surface appearing minutely granulose until near end where faint radial sculpture becomes visible. Postnuclear sculpture as in nominate race. Umbilicus 'U'-shaped, slightly decoiling until body whorl, contained 3·52–4·15 times (mean 3·71) in the diameter, margins strongly rounded. Sutures impressed, whorls strongly rounded above, compressed laterally. Parietal wall with single median lamella extending posteriorly more than one-quarter whorl, high and markedly bifid on posterior quarter with gradual descension to threadlike anterior quarter or third. Columellar wall without dentition. Palatal wall with single, high, sinuately twisted lamella, expanded above, extending posteriorly almost one-quarter whorl, located just below baso-columellar margin.

Afrodonta bilamellaris londonensis differs from the nominate race in its much larger palatal and parietal denticles, plus its slightly smaller size. Differences from other species are covered in the diagnosis of the nominate race.

Description. Shell small, with 4¼ tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0·524. Apical whorls about 1⅜, slightly swollen near end, surface appearing granulose under 96× magnification. Postnuclear whorls with very fine radial ribs that are not clearly separable from microriblets over much of surface, vague microspirals visible. Sutures deep, whorls strongly rounded above, compressed laterally with evenly rounded outer margin, strongly rounded basally, umbilical margin strongly rounded. Umbilicus 'U'-shaped, regularly decoiling until last part of body whorl, contained 3·57 times in the diameter. Parietal wall with median lamella extending posteriorly almost to line of vision, broadly bifid posteriorly with gradual descension to anterior threadlike portion. Columellar wall without dentition. Palatal wall with single basal lamella extending posteriorly for one-quarter whorl, strongly expanded and sinuately twisted above with rather sharp descension to top of basal callus. Height of holotype 0·71 mm, diameter 1·35 mm.

Holotype. Signal Hill, East London, Cape Province. Collected by S. Kincaid. Natal Museum.

Material. Signal Hill, East London (4 specimens, NM, FMNH 159054).

Remarks. The slightly smaller size of *A. b. londonensis* probably correlates with the greatly increased tooth prominence. A few individuals of the nominate race showed an elongated and bifid parietal, but the majority have a simple parietal and very small palatal. All four examples from Signal Hill have a huge parietal and greatly enlarged palatal. There is a large gap between the lamellar size in the largest nominate *bilamellaris* and the smallest parietal in *londonensis*. Because there are no major shell differences and the tooth shape is basically the same, I am considering the difference as subspecific.

Afrodonta unilamellaris Connolly, 1933

Afrodonta unilamellaris Connolly, 1933. Ann. Natal Mus., 7 (2): 146, pl. VII, figs. 2–4. Mfongosi, Zululand. —Connolly, 1939. Ann. S. Afr. Mus., **33**: 250–251, fig. 19 (6).

Diagnosis. Shell smaller than average, diameter 1·23–1·50 mm (mean 1·41 mm), with $3\frac{7}{8}$ to $4\frac{1}{4}$ tightly coiled whorls. Apex and spire slightly to moderately and evenly elevated, spire protrusion about one-seventh body whorl width, last whorl descending more rapidly, H/D ratio 0·471–0·533 (mean 0·500). Apical whorls about $1\frac{3}{8}$, slightly swollen, macroscopically smooth, best preserved examples with vague microreticulation under 96× magnification. Postnuclear sculpture as in *A. connollyi*, without clear separation into major and micro elements. Umbilicus narrowly open, 'U'-shaped, regularly decoiling, contained 3·72–4·50 times (mean 4·14) in the diameter, margins strongly rounded. Whorls strongly flattened laterally and slightly less so basally. Parietal wall with single median to submedial, short, low, cord-like lamella extending posteriorly slightly more than one-eighth

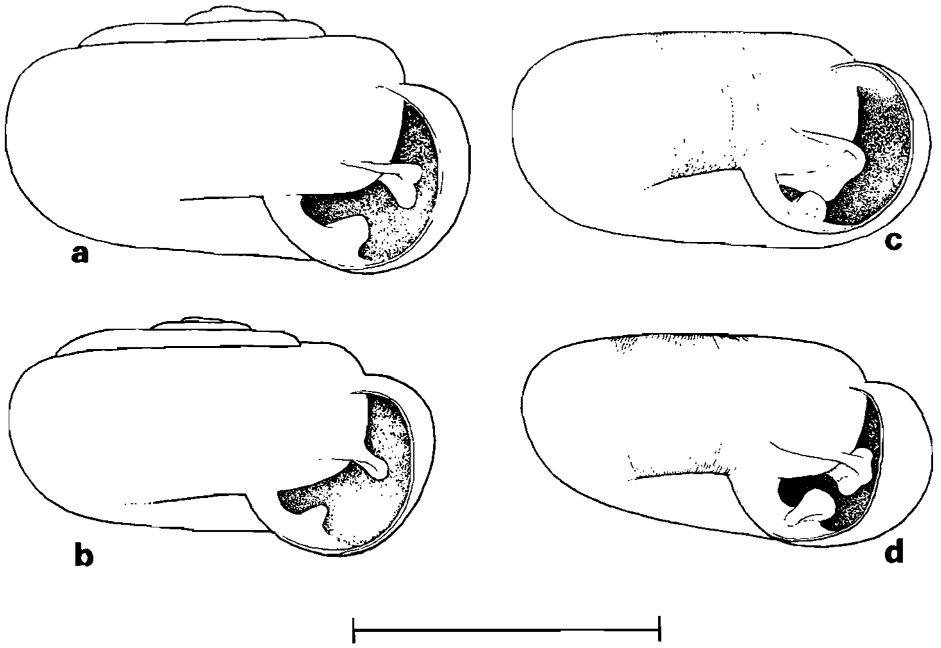

Fig. 2. *Afrodonta bilamellaris bilamellaris* Melvill & Ponsonby, from Dargle, Natal: *a–b*, variation in parietal lamellae. *Afrodonta bilamellaris londonensis*, new subspecies, holotype from Signal Hill, East London, Cape Province: *c–d*, side views showing parietal lamellae from different angles. Scale line equals 1 mm.

whorl, occasionally split and narrowly separated with a connecting callus. Columellar and palatal walls without dentition.

Afrodonta unilamellaris is almost identical in shape and size to *A. connollyi*, but the latter has two very large parietals and is slightly larger.

Holotype. Mfongosi, Zululand. Collected by W. E. Jones. British Museum (Natural History) number 1931.6.4.3.

Material. Mfongosi (34 specimens, NM, BMNH 1931.6.4.3, BMNH 1937.12.30. 2795–03, FMNH 159049).

Remarks. Differences between *A. connollyi* and *A. unilamellaris* involve primarily the two very large parietals of the former contrasted with the single low cord of the latter. No transitional material was seen and I have no hesitation in considering them to be distinct.

Afrodonta introtuberculata Connolly, 1933

Afrodonta introtuberculata Connolly, 1933. Ann. Natal Mus., **7**: 147–148, pl. VII, figs. 5–8. Nottingham Road, Natal.—Connolly, 1939. Ann. S. Afr. Mus., **33**: 255–256, fig. 19(9).

Diagnosis. Shell very large, diameter 1·81–1·96 mm (mean 1·89 mm), with 5 to 5$\frac{3}{8}$ tightly coiled whorls. Apex and spire slightly sunken, moderately overlapped by preceding whorls, body whorl not descending to level of spire, H/D ratio 0·403–0·495 (mean 0·424). Apical whorls nearly smooth, only very faint traces of microreticulation visible in sutures, on rest appearing as faint granulosities. Postnuclear whorls with narrow, moderately prominent, vertically sinuated radial ribs, about 135 on the body whorl, whose interstices are equal to their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, with faint traces of microspiral riblets visible between. Umbilicus shallow, cup-shaped, regularly decoiling, contained 2·49–2·80 times (mean 2·70) in the diameter. Sutures deep, whorls slightly compressed laterally above and below periphery, strongly rounded above and at umbilical margins. Parietal and columellar walls without dentition. Palatal wall with two small tubercles, generally recessed one-quarter whorl from aperture. Lower tubercle near baso-columellar margin, upper tubercle slightly more deeply recessed and slightly supraperipheral in position.

Afrodonta introtuberculata is immediately separable by its slightly depressed spire, relatively prominent radial ribbing, large size, and in possession of only two small and deeply recessed palatal tubercles. *A. inhluzaniensis* has a distinctly elevated spire, much narrower umbilicus, and two large lamellae that are located near the aperture. Both *A. kempi* and *A. bimunita* have large transverse palatal structures, the former additionally having a much narrower umbilicus, protruding spire, and greater H/D ratio, while the latter has a much more depressed spire and much more highly developed dentition.

Holotype. Nottingham Road, Natal. Collected by A. J. Taynton. British Museum (Natural History) number 1931.6.4.1.

Material. Nottingham Road (78 specimens, NM, BMNH 1931.6.4.1, BMNH 1937.12. 30.2759–61, FMNH 159047).

Remarks. Examination of the large type lot series in the Natal Museum shows that denticle development in *Afrodonta introtuberculata* departs radically from the typical endodontid pattern. Viewed by strong reflected light, the tubercles are clearly visible as whitish lumps, the upper slightly more deeply recessed than the lower. Their relative position normally is three-sixteenths to one-quarter whorl behind the lip edge, most specimens being nearly one-quarter whorl. In 2 of 47 shells, there is an inner pair of tubercles that are reduced in diameter and located almost three-eighths whorls back and either just the lower or both tubercles (one in each situation) present in a second set located about one-eighth whorl behind the aperture. Rather than the normal continual anterior addition and posterior absorption of the denticles, *A. introtuberculata* shows building of a denticle pair at quarter whorl intervals coinciding or followed by resorption of the previous set.

Afrodonta inhluzaniensis (Burnup, 1912)

Endodonta (*Afrodonta*) *inhluzaniensis* Burnup, 1912. Ann. Natal Mus., **2**: 342–343, pl. XXIV, figs. 14–17. Inhluzani Mt., Natal.—Connolly, 1912, Ann. S. Afr. Mus., **11** (3): 128.

Afrodonta inhluzaniensis (Burnup). Connolly, 1939. Ann. S. Afr. Mus., **33**: 251–252, fig. 19(5). Van Reenen, Natal.

Diagnosis. Shell smaller than average, diameter 1·33–1·51 mm (mean 1·43 mm), with 3¾ to 4⅜ tightly coiled whorls. Apex and spire strongly and evenly elevated, body whorl descending a little more rapidly, spire protrusion about one-third body whorl width, H/D ratio 0·523–0·663 (mean 0·584). Apical whorls with only faint granulosities showing, sculpture on postnuclear whorls reduced to very fine microradial and much finer spiral riblets, becoming slightly stronger near aperture. Umbilicus rather narrow, 'U'-shaped, slightly decoiling, contained 3·60–4·60 times (mean 4·21) in the diameter. Sutures moderately impressed, whorls evenly rounded on outer margin, slightly flattened laterally below periphery with strongly rounded basal margin. Parietal and columellar walls without dentition. Palatal lamellae 2, extending less than one-eighth whorl, lower palatal at basocolumellar margin a very broad and rounded, cord-like tooth, slightly recessed within aperture, with sharp anterior descension; upper palatal slightly subperipheral in position, base narrower, crescent-shaped, becoming broadly rounded above, with sharp to gradual anterior descension.

Afrodonta inhluzaniensis has 2 short and broad palatal lamellae, a protruded spire, narrow umbilicus and large H/D ratio. Of the other species with only palatal dentition, *A. introtuberculata* has a very wide umbilicus, low spire and is much larger with the palatals deeply recessed; *A. bimunita* has a deeply depressed spire and two rows of palatal tubercles; and *A. kempi* has recessed calluses.

Holotype. Inhluzani Hill, Dargle district, Natal. Collected by H. C. Burnup. British Museum (Natural History) number 1912.3.25.2.

Material. Van Reenen (24 specimens, NM, BMNH 1937.12.30.2755–8, FMNH 159050); Inhluzani Hill, Dargle district (4 specimens, NM, BMNH 1912.3.25.2); Mkolombe Mt. (24 specimens, NM); Cathkin Peak, Drakensberg Mts. (2 specimens, Indumeni Forest, Cathedral Peak area, 4,800', Drakensberg Mts. (31 specimens, NM, FMNH 159053).

Remarks. While there are indications of local differences in spire protrusion (reflected in H/D ratios, see Table II), the several local populations agree quite closely in size and umbilical characters. There is considerable variation in exact shape and size of the palatal lamellae. Variation within each sample was large enough that I could detect no clear differences between populations.

Afrodonta kempi (Connolly, 1925)

Endodonta kempi Connolly, 1925. Ann. Mag. Nat. Hist. (9), **15**: 472–473, pl. 28, fig. 13. Igembi Hills, Kenya at 6,000′ elevation.

Description. Shell large, with 4½ very tightly coiled whorls. Apex and spire barely emergent, body whorl descending slightly more rapidly, H/D ratio 0·566. Apical whorls 1½, first 1¼ whorls globosely swollen, latter portion narrowing rapidly. Apical sculpture of very faint microreticulation. Postnuclear whorls with sculpture of very fine and crowded microradial riblets crossed by even finer and more crowded spiral riblets. Sutures deep, strongly rounded above and on basal margin, with evenly rounded, laterally compressed outer margin. Umbilicus narrowly 'U'-shaped, barely decoiling, contained 3·66 times in the diameter, with slightly shouldered margins and spiral sculpture more strongly developed inside. Parietal and columellar walls without dentition. Palatal wall with two transversely slanting, ridgelike calluses and a deeply recessed, low, posterior tubercle. Anterior callus recessed one-sixteenth of a whorl, high, broadly rounded with sharp anterior and posterior descension, starting near baso-columellar margin and slanting backwards up palatal wall at about a 15° angle from shell axis; posterior callus recessed three-sixteenths of a whorl, similar in shape and form to the anterior, but slanting at a slightly greater angle across the wall; tubercle recessed slightly more than one-quarter whorl, situated at baso-columellar margin. Height of holotype 0·99 mm, diameter 1·75 mm.

Holotype. Igembi Hills, Kenya, at 6,000 ft elevation. Collected by Kemp. British Museum (Natural History) number 1937.12.30.2762.

Material. Nufenguri, Kenya (1 specimen, B. Verdcourt).

Remarks. The palatal callus form agrees with that found in the New Zealand *Ptychodon blacki* complex. *Afrodonta kempi* is undoubtedly a parallel local derivative of *Trachycystis* stock. The two parallel calluses show intriguing similarities in position to the tubercles seen in *A. bimunita.* The two species differ in the spire elevation, smaller size, and fatter body whorl of the former.

Only the holotype and single dead specimen collected by John G. Williams are known. There are slight differences in the palatal callus recession. This probably indicates the same growth pattern inferred for *A. bimunita.*

Afrodonta bimunita Connolly, 1939

Afrodonta bimunita Connolly, 1939. Ann. S. Afr. Mus., **33**: 256, fig. 19, pl. VI, figs. 1–4—Hogsback, Amatola Mts., Cape Province.

Diagnosis. Shell very large, diameter 1·97 mm, with 5¼ tightly coiled, widely overlapping whorls. Apex and spire deeply sunken, last three-eighths of body whorl descending to level of penultimate, H/D ratio 0·591. Apical whorls macroscopically smooth, with faint traces of microreticulation visible under high magnification. Postnuclear whorls with prominent, narrow, vertically sinuated radial ribs, 152 on the body whorl, whose interstices are 1½ to 2 times their width. Very fine microreticulation visible between ribs with spiral secondary ribbing strongly developed in umbilicus. Umbilicus deep, 'V'-shaped, regularly decoiling, contained 3·24 times in the diameter. Sutures shallow, whorls strongly rounded above and on basal margin with evenly rounded, crescentic, laterally compressed outer margin. Parietal and columellar walls without dentition. Palatal wall with two slightly 'V'-shaped rows of five tubercles each: first row recessed one-eighth whorl from aperture, lowest tubercle most posterior, middle two most anterior in position; 2nd row of tubercles recessed almost one quarter whorl from aperture. All tubercles slightly longer than wide, almost evenly distributed along palatal wall.

The markedly depressed apex and large size immediately separate *Afrodonta bimunita* from other toothed African species. *A. kempi* is smaller, has an elevated spire and the rows of tubercles are replaced by transverse palatal calluses.

Holotype. Hogsback, Amatola Mountains, Cape Province. Collected by Lawrence. South African Museum.

Material. Hogsback, Amatola Mountains (1 specimen, BMNH 1937.12.30.2726).

Remarks. The deeply sunken apex and strong overlapping of the lower whorls strongly recall the New Zealand and Tasmanian *Geminiropa.* The South African species obviously differs in the form of the dentition and in sculptural detail. These are parallel developments. The difference in palatal tooth recession between the holotype (see Connolly, 1939: pl. 6, figs. 1, 3, 4) and paratype described above suggests a pattern of replacement and then absorption instead of continual addition anteriorly and resorption posteriorly.

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